

## BIRDS OF BASS STRAIT

## Evolution and Ecology of the Avifaunas of some Bass Strait Islands, and Comparisons with those of Tasmania and Victoria

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**ABSTRACT:** Up to about 18,000 years ago when Tasmania was a peninsula of Australia, the exposed Bass Strait plain was probably important in the evolution and ecology of Bird species at present endemic to the Tasmanian region. The large Bass Strait islands and Tasmania have 12%-17% of their species not shared with the mainland, a high figure compared with that of the other Australian offshore islands. It is difficult to attribute this unequivocally to distance from the nearest mainland or age of the islands. The Bass Strait islands and Tasmania have only 15%-50% of the passerine species breeding in Southern Victoria. A plot of number of breeding forest passerines on these islands against island area  $A$  does not adequately approximate the equation  $S = kA^z$ , especially for islands smaller than about 40 km<sup>2</sup>. This, and other evidence, points to passerine species having very low immigration and invasion rates onto islands. The pattern of distribution of land bird species on the islands is largely relict. A provisional scheme of their evolutionary history in the Tasmanian region of Bass Strait is proposed. Fifty-one species are postglacial intrusives into Southern Victoria.

It is unnecessary to fall back on competitive exclusion to explain the impoverishment of the island avifaunas. There is no convincing evidence that on the Bass Strait islands and Tasmania passerine species change in bill and leg dimensions to exploit unfilled niches. Some populations of the same species differ from island to island in their feeding zonation, suggesting intrinsic but as yet unresolved differences in food supply. Absence of mainland bark-probing species from the Tasmanian region of the Strait does not satisfactorily explain why only some island populations of some species feed from bark. A similar lack of evidence for changes in morphological variation (bill length, tarsal length) of island populations of passerines suggests that the theoretical importance given to competitive processes warrants evaluation.

## INTRODUCTION

Frequent questions about bird populations on islands are whether, and if so why

1. Islands have fewer species than comparable areas of adjacent mainlands.
2. Islands have fewer congeneric species than an equivalent area of mainland.
3. The distance from an island to the nearest mainland influences the rate of colonization, and the size of the island affects the rate of extinction of species.
4. Bird species on islands have longer bills and legs, and/or a wider range of variation in bill size and tarsal length, than mainland species.
5. Bird species on islands have more generalized

habits, such as the wide range of sizes of food items taken and of habitats occupied.

Such questions have been given serious attention by Grant (1965, 1966a), MacArthur and Wilson (1967) and Lack (1971).

Bird populations of Australian offshore islands (of which there are about 1300 (Anon. 1912)) have up to now escaped such detailed analyses. Early this century when taxonomy for its own sake was in vogue (Campbell 1900, Mathews 1912), visitors to islands went there solely to seek new species or subspecies. A happy by-product was that many lists of the birds found there were published (bibliography in Abbott 1972). These have been invaluable aids for com-

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parisons by later visitors. The larger islands in Bass Strait, as well as Tasmania, were often visited by members of the Royal Australasian Ornithologists' Union and the Field Naturalists' Club of Victoria, probably because these organizations were based in Melbourne. Modern lists, also, of birds of the islands in Bass Strait have been compiled by workers more specifically interested in the distribution and abundance of species. These form a basis for a study of the ecology and evolution of passerine bird species in particular.

On the basis of the axiom that no two species can co-exist for long before one acquires numerical superiority over the other, workers such as Grant (1965, 1966a), MacArthur and Wilson (1967) and Lack (1971) hold that competitive processes are the keynote to an understanding of the ecology and evolution of bird species on islands. From this same viewpoint, Ridpath and Moreau (1966: 372) explain why Tasmania has fewer bird species than equivalent Victorian habitats. None of these workers, however, adequately consider another aspect: that Bass Strait was and is a substantial physical barrier separating many Victorian species from Tasmania and the Bass Strait islands.

Such a 'barrier viewpoint' can be elaborated to serve as a basic model of probable history for the birds of the islands in Bass Strait and of Tasmania, especially to explain the high degree of species endemism, and on the islands the impoverished avifaunas. In this paper, such a model is tested with data from the literature and discussed in terms of the views of Ridpath and Moreau (1966) and of Lack (1971).

## ENDEMISM

It has long been noted (e.g. Flinders 1801) that islands hold more endemic species than continental areas many times their extent. To pursue this observation the bird species restricted to King, Flinders, Cape Barren and Deal Islands and Tasmania are here tabulated (Table 1), and the question of Tasmanian influence on the high number of endemic bird species held by the Bass Strait islands is considered. Also, the numbers of such endemic species found in other animal groups, and of plant families that dominate the vegetation of the larger islands are listed (Table 2) to see which parallels there are, if any. To determine which factors might decide the number of endemic bird species on an island, lists of parameters for other Australian islands are given (Table 3). Data from overseas areas are quoted where relevant.

Tasmania and the islands in Bass Strait, being continental islands, have been alternately joined

to, and separated from Victoria throughout the Pleistocene (Jennings 1971). Some bird species have reached Tasmania during an early glacial and evolved in isolation during the subsequent interglacial (Serventy 1967a). During the later glacial, a similar species has reached Tasmania. Two such species are known as members of a double invasion. Because of the position of the islands in Bass Strait, it is of interest in reconstructing the Pleistocene botany to note whether the older or newer members of the double invasions are present.

## 1. IMPORTANCE OF TASMANIA

To avoid clumsy circumlocutions, I shall use 'Tasmania (s.l.)' to refer to the situation in the past when Tasmania was a peninsula of Australia, incorporating all of the present Bass Strait islands into a land bridge. The term 'island endemic' will designate species restricted to a single island. Species restricted to two or more islands are called 'island group endemics'. Because only three of the Australian continental islands have endemic bird species that fit the first category (Table 3, last column), little more will be said of this class.

A list of the bird species endemic to the Tasmanian region is given in Table 1. These endemics must have arisen in one of two ways. They either originated in Tasmania (s.l.) (neoendemics) or they originated on the Australian mainland, spread to Tasmania (s.l.), and have since died out on the mainland (relict endemics). For the neoendemics, it is necessary to establish if they originated before or after about 13,000 years ago, when the land link to Tasmania was finally broken (Jennings 1971). Those that evolved after this time may not have gained access to the mainland. On the other hand, those that evolved earlier on Tasmania (s.l.) should have reached the mainland because there is no evidence of any physical barrier that would have prevented their movement northward. In this case, their absence today from the mainland indicates that they are secondarily relict endemics. However it is not conclusively known in which way any of the 13 Tasmanian region endemic species originated.

At the height of the last glaciation, some 20,000 years ago, about 52,000 km<sup>2</sup> of ground to the north of Tasmania was above sea level (Abbott 1972), and presumably vegetated. Because the 100 m isobath W. and E. of Tasmania lies only 15-20 km from the present shoreline, little extra land was added in these places. Over 80% of Tasmania lies above the 300 m contour, and with a 5°C drop in temperature the tree line would



have been lowered to 500 m above sea level (Galloway 1965) or 300 m (Davies, quoted by Ridpath and Moreau 1966, p. 359). Thus much of Tasmania would have been covered with habitat which today is inimical to most bird species. The drier *Eucalyptus* forests where most of the endemics are very common today (pers. obs.) would have been greatly reduced in extent. However, presumably the remainder of Tasmania (s.l.), being at a lower latitude and altitude, was covered with *Eucalyptus* dominated habitats. The Bass Strait area during the last glacial was probably the focal point of the distribution and abundance of the species which are at present endemic to the Tasmanian region.

Ridpath and Moreau (1966: 385) reasoned that because many of the Tasmanian region endemic species are scarce or absent in *Nothofagus/Phyllocladus* habitat, they entered Tasmania later than about 18,000 years ago. Further, because some of these species occur on King Island (which became an island about 11,000 years ago), such species must have originated between 18,000 and 11,000 years ago. If this is so, argue Ridpath and Moreau, these species existed while the eastern side of Bass Strait was still a land bridge, with no known barrier to movement into Victoria. Because the species are unknown in Victoria, Ridpath and Moreau assume that the endemics did survive the glaciation in Tasmania after all, thus contradicting their original premise. They do not consider that the endemics could be relict. However, Serventy (1967b) argues against the likelihood of species evolved on islands successfully colonizing a mainland. He follows Darwin in postulating that species evolved on large land masses have a competitive advantage over others not so evolved. But this postulate ignores the fact that as a result of past climatic changes, the Australian mainland avifauna has many times been broken up into a series of isolates (Keast 1961).

My interpretation is that the presence of Tasmania may not have made much difference to the production of bird species that are at present endemic to Tasmania and the Bass Strait islands. However, Tasmania may have provided some of the basic stocks which differentiated during interglacial stages on the exposed Bass Strait plain.

## 2. ENDEMISM IN OTHER GROUPS

Investigations were made to establish any consistent patterns in endemism among plant and animal groups in the Tasmanian region. Data for four prominent families of plant species, and for mosquitoes, amphibians, reptiles, birds and mammals are presented in Table 2. The plant families Mimosaceae, Myrtaceae, Proteaceae and Epacri-

daceae are prominent in much of the vegetation of Tasmania, the Bass Strait islands, and Victoria. Mimosaceae and Myrtaceae contain the genera *Acacia* and *Eucalyptus*, of obvious importance in the habitat of forest birds.

Only three of the taxa listed in Table 2 have Tasmanian endemics on the Bass Strait islands. These are Proteaceae, Reptilia and Aves. The absence of any uniform pattern surely indicates the taxa have had very different places of origin and subsequent dispersal and distribution. A little is known of the latter for some taxa, e.g., in the past some of the Tasmanian endemic mammals have occurred in the Furneaux and Kent groups (Hope 1969).

Birds are the only group to have endemic species shared with Tasmania present on all the major islands in Bass Strait (Table 2). However, it is surprising that King Island should have a higher percentage of endemic bird species than the Furneaux Group, wherein the largest island (Flinders Island) is about 200 km<sup>2</sup> larger than King Island. Also, King Island does not have the topographic diversity that Flinders Island has (highest points are 210 and 750 m respectively), nor does it have the variety of habitats or number of plant species that Flinders Island has (pers. obs.). This indicates that these factors, usually given *prima facie* importance in island studies, are irrelevant in explaining the discrepancy.

## 3. COMPARISON WITH OTHER AUSTRALIAN CONTINENTAL ISLANDS

The number of endemic bird species that an island has today is related to the age of the island. If young, there may have been insufficient time for endemic species to evolve (or for species shared between the island and mainland to become extinct on the mainland). If old, endemic species may have become extinct or established on the mainland. This time factor is probably modified according to the ecology of the island. We can therefore attempt to assess the potency of a number of easily measured factors in explaining differences in the number of endemic bird species on islands around Australia.

Factors considered are (1) minimum distance at present separating an island from the mainland, (2) area and greatest height as a measure of the ecology of the island, and (3) time of isolation (calculated from a graph in Hails 1965). These data, along with the number of bird species not shared with the mainland and the number of bird species restricted to each island, are listed for all the major islands in Table 3. Apart from Tasmania and the islands in Bass Strait, only three islands (Kangaroo, Dirk Hartog and Barrow)

hold species (one each) which are absent from any mainland. This is less than 5% of the avifauna of these islands, and is much lower than the figure (12%-17%) for Tasmania and the large Bass Strait islands (Table 2). Although Tasmania has numerically more non-mainland species than any other Australian island, King Island has proportionately more, both for its area and avifauna (Tables 2, 3).

Only three islands have species that are restricted to one island (one island endemics). These are King and Kangaroo Islands and Tasmania (Table 3, last column). With the data assembled (Table 3), it is difficult to separate distance of island from mainland and age of island, because the islands with most endemics are generally farthest from the mainland, and are also the oldest. Furthermore, some islands (Barrow, Dirk Hartog, Kangaroo) which have been separated from the mainland only a short time also have endemic species.

The oldest island, but not the one that is most distant from the mainland, is King Island (Littlejohn and Martin 1965) (Table 3). Of the species in its avifauna 17% are not shared with the mainland. The next oldest large islands—Flinders, Cape Barren and Tasmania—have about 12% of the species in their avifauna endemic. The modifying effect of island size and ecology is apparent in the case of Deal Island and the islands of Houtman Abrolhos. Because Deal Island (in the Kent Group) lies within the 55m isobath, the Kent and Furneaux Groups were part of one large island until the sea had risen to about the 35m isobath, that is for approximately 1000 years (Abbott 1972). During this time these groups probably shared avifaunas, so that the absence from Deal Island today of eight of the Tasmanian region endemics which are on Flinders Island is probably due to extinction. This is not surprising, since Deal Island is about 1% of the area of Flinders Island. On the other hand, King Island has separated from Tasmania with most of the Tasmanian region endemics.

Although Houtman Abrolhos was the next island group to be separated from the mainland, it consists of numerous small, low islets which would not be expected to support endemic species.

Lack (1970) has argued against the view that endemism in island birds is correlated with isolation, which he takes to be represented by distance from the mainland. Data in Table 3 support Lack, since some large, close islands (Dirk Hartog, Kangaroo) have endemic species while islands of similar size, but more distant (Melville, Groote) do not. These large islands are

0.5-5 times the area of King Island (Table 3). Isolation, represented by age of the island, may be a more realistic parameter, though the correlation again is not perfect. For example, Bernier Island has one endemic, but the older Melville island has none. Very old non-continental islands (isolated before 18,000 years ago), such as Lord Howe, Norfolk, and New Zealand have about 50-60% of their avifauna endemic (Abbott 1972). However these islands are also far from the nearest mainland. Madagascar, which is only 405 km from Africa, has 70% of its avifauna endemic. The minimum depth of the intervening strait is over 1000m, implying long isolation (Moreau 1966).

#### 4. MULTIPLE INVASIONS AND COLONIZATIONS

Multiple invasions are cases where two or more closely related species occur on the Bass Strait islands and/or Tasmania with only one existing on the mainland (Mayr 1942). The first invading species diverges most from the mainland stock, and is the species not found today in Victoria. The newer invader is sufficiently different from the first not to interbreed; it is the species found today on mainland Victoria. Where there are two closely related species on the mainland, the situation may be called a double colonization. Serventy (1967a) discussed two examples in detail—*Acanthiza ewingi* and *A. pusilla* (double invasion), and *Strepera graculina* and *fuliginosa*, and *S. versicolor* and *arguta* (double colonization). Serventy conjectured that the older member of the double invasion or colonization alone occurs on the Bass Strait islands. New information, not available to Serventy, is summarized in Appendix Table 1A.

The older invaders which are present on the islands in Bass Strait are *Pardalotus quadragintus*, *Acanthiza ewingi*, *Melithreptus affinis*, *Acanthornis magnus*, *Sericornis humilis*, *Platycercus caledonicus* and *Strepera fuliginosa*. The newer invaders occurring on these islands are *Pardalotus punctatus*, *Acanthiza pusilla*, *Melithreptus lunatus*, *Sericornis frontalis* and *Platycercus elegans*. Thus, *Strepera fuliginosa* is the only case where the older invader is found alone on the Bass Strait islands.

It has been suggested that at the time of isolation of the Bass Strait islands, they supported mostly rainforest/wet sclerophyll habitats (Green 1969). The evidence from double invasions of bird species militates against this view because the new invaders are not indicative of wetter habitats, and they are as widespread on the Bass Strait islands as are the older invaders.



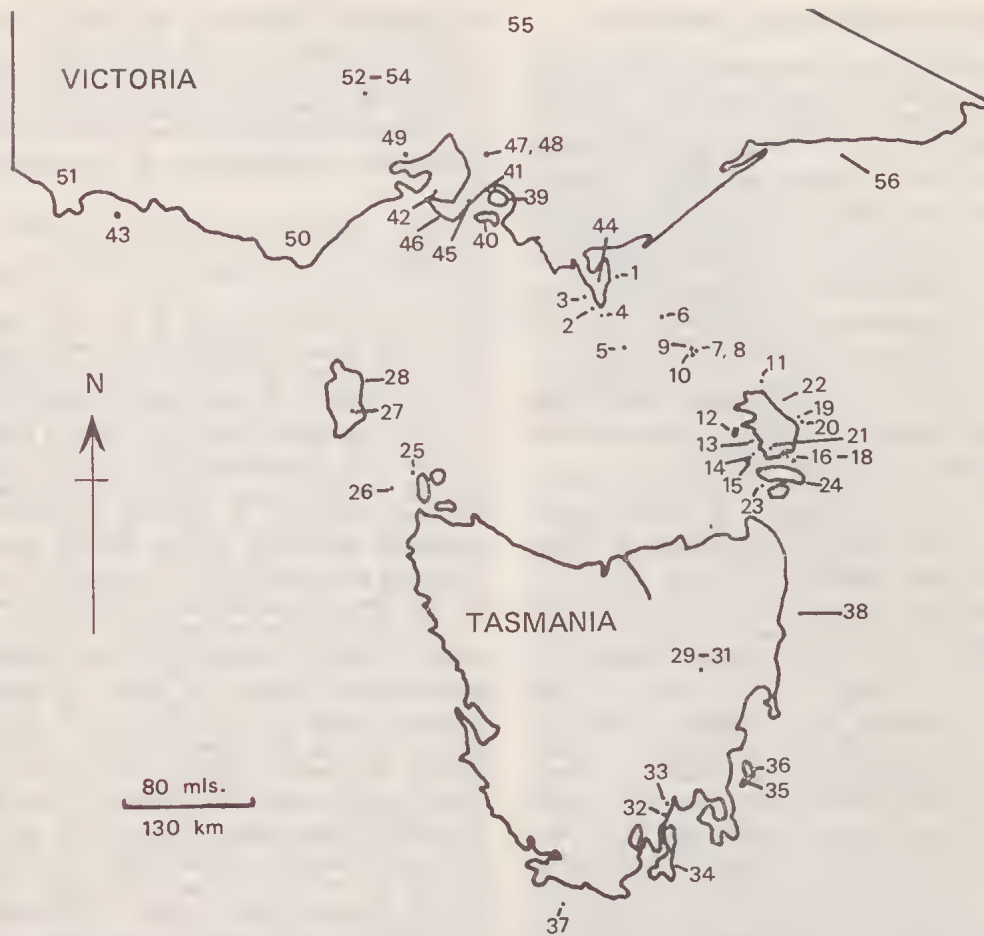


FIG. 1: Location of areas used in Figure 2

**ISLANDS:** 1. Clifly Island (D. F. Dorward, pers. comm.). 2. Anser Island (D. F. Dorward, pers. comm.). 3. Great Glennie Island (D. F. Dorward, pers. comm.). 4. Rodondo Island (Bechervaise, 1947). 5. Curtis Island (Abbott, unpubl.). 6. Hogan Island (N. Scarlett, *in lit.*). 7. Deal Island (pers. obs.). 8. 10 acre plot, Light-house Gully, Deal Island (pers. obs.). 9. Erith Island (Whinray, 1971). 10. Dover Island (Whinray, 1971). 11. West Sister Island (Whinray, 1972). 12. Prime Seal Island (D. Milledge, unpubl. list). 13. Big Green Island (Norman, 1970). 14. Mt. Chappell Island (D. Milledge, unpubl. list). 15. Badger Island (D. Milledge, unpubl. list). 16. Fisher Island (Guiler, Serventy and Willis, 1958). 17. Tinkettle Island (D. Milledge, unpubl. list). 19. Babel Island (D. Milledge, unpubl. list). 20. Cat Island (Cashion, 1958). 21. 10 acre plot, Smiths Gully, Flinders Island (pers. obs.). 22. Flinders Island (pers. obs., Green, 1969, 1971). 23. Preservation Island (D. Milledge, unpubl. list). 24. Cape Barren Island (D. Milledge, unpubl. list; Whinray, 1970). 25. Albatross Island MacDonal and Green, 1964). 26. Black Pyramid (Green and MacDonald, 1964). 27. 10 acre plot, Rafferty's Gully, Pegarah Forest Reserve, King Island (pers. obs.). 28. King Island (pers. obs.; Green and McGarvie, 1971). 29.-31. Four 5 acre plots, Campbell Town, Tasmania (Recher, Thomas and Milledge, 1971). 32. 10 acre plot, east side Mt. Louis (pers. obs.). 33. Mt. Wellington area (D. Milledge, unpubl. list). 34. Bruny Island (McGilp and Parsons, 1924; Mosey, 1947; D. Milledge, unpubl. list). 35. 10 acre plot, NE. of Chinamans Bay, Maria Island (pers. obs.). 36. Maria Island (D. Milledge, unpubl. lists; Temple-Smith, 1968). 37. Maatsuyker Island (D. Milledge, in press in *Emu*). 38. Tasmania (Sharland, 1958). 39. French Island (Quin, 1969). 40. Phillip Island (Pound, 1969). 41. Quail Island (Hyett and Gottsch, 1963). 42. Mud Islands (R. Wheeler, unpubl. list). 43. Lady Julia Percy Island (Pescott, 1965).

**MAINLAND AREAS:** 44. Wilsons Promontory (Anon, 1970; Barrett, 1920, Bryant, 1930; Kershaw, 1906; Mars-ton, 1969; Pescott, 1967; Quin, 1970; St. John, 1909; Wheeler, unpubl. list; pers. obs.). 45. Somers area, Mornington Peninsula (A. J. Reid and W. A. Davis, unpubl. list). 46. Mornington Peninsula (Wheeler, 1967). 47. Dandenong Ranges area (R. Wheeler, in press). 48. Churchill National Park (Bliss, 1969). 49. You Yangs (Hore-Lacy, 1959, 1965). 50. Otway area (Hill, 1902; Wheeler, 1967; Johnson, 1967, pers. obs.). 51. Portland area (Learmonth, 1966). 52.-53. 10 and 20 acre plots, Coates Gully, St. George's Lake, and Diamond Gully, Creswick. 54. Creswick district (R. Cowley, unpubl. list). 55. Strathbogie Ranges (Bedggood, 1972). 56. Vic-toria (Wheeler, 1967).

## AREA AND NUMBER OF SPECIES

Many attempts have been made to see which factors about islands are most important in determining how many bird species they support. The work of Hamilton et al. (1964) and MacArthur and Wilson (1967) suggests area to be a potent factor, and other factors such as elevation and isolation to be relatively unimportant. Moreau (1966: 359) suggested that the following factors need to be accounted for in explaining the number of species an island has: (1) the history of each island, (2) its degree of isolation; (3) the complexity of habitats it carries, (4) the extent to which its habitats and its bird fauna have suffered from human interference, and (5) the completeness with which the avifauna is known.

Factor (4) has probably affected Hogan Island and some of the small islands in the Furneaux Group, and soon will be of importance for King Island. I do not consider that factor (5) is of major importance for any island except Rodondo Island. MacArthur and Wilson (1967:8) believe that island area may be an adequate measure of (3). Fig. 2 is a graph (on log scale) of the number of breeding (or presumed breeding) passerine species plus one ( $S$ ) against island area ( $A$ ). The geographical areas used are shown in Fig. 1. Species considered are those that breed in *Eucalyptus* forest and/or heath, and which belong to the families Dicaeidae, Climacteridae, Neosittidae, Acanthizidae, Maluridae, Rhipiduridae, Monarchidae, Muscicapidae, Pachycephalidae, Falcunculidae and Meliphagidae as defined by Condon (1969). Unqualified use of the term 'species' in the remainder of this section is meant to indicate breeding species in these families only. Because some islands have none of these species breeding, I have avoided log (0) by transforming the number of species  $N$ , to  $N + 1$ . Also included in Fig. 1 are points for areas in mainland Victoria, ranging from 10 acre (0.04 km<sup>2</sup>) plots to the whole area of Victoria. I have also included points for French, Quail, Phillip, Mud, Lady Julia Percy, Bruny, Maria, and Maatsuyker islands.

MacArthur and Wilson (1967, Ch. 2) hold that a rough approximation for number of species,  $S$ , in an island fauna is given by  $S = kA^z$ , where  $k$  and  $z$  are empirically determined constants and  $A$  is area. With such a relationship,  $ds/S = z dA/A$ , so that for a given increase in area, species number will always increase in the same ratio. The validity of this equation for areas larger than 1 ml<sup>2</sup> (9.59 km<sup>2</sup>) is supported by graphs in MacArthur and Wilson (1967: 8, 10 and 23). However when areas are less than 100 acres (0.40 km<sup>2</sup>), it is evident that  $S = kA^z$  does not

hold (graph in MacArthur and Wilson 1967: 32).

My data for the Bass Strait islands (Fig. 2) show that  $S = kA^z$  does not hold over the whole range of  $A$ , especially for small and large islands, and for small mainland areas. For the islands the species/area relation might be represented better as

$$\begin{aligned} S &= 0 && \text{for } A < c. 10^3 \text{ acres (c. } 4.0 \text{ km}^2\text{);} \\ S &= kA^z && \text{for } c. 10^3 < A < c. 10^4 \text{ acres;} \\ S &= k'A^{z'} && \text{for } A > c. 10^4 \text{ acres (c. } 40.5 \text{ km}^2\text{)} \end{aligned}$$

That is, in the lower part of the area range, the size of an island below which no breeding passerines are present is a little less than 1000 acres (4 km<sup>2</sup>). Islands of area between about 1000 and 10,000 acres show a rapid increase in number of species with increasing area, while in the upper part of the area range, the rate of increase drops off markedly (Fig. 2). Possible explanations are discussed later. Fig. 2 very clearly shows that islands of comparable size to a mainland area have far less than the mainland quota of species.

Two explanations are possible, after MacArthur (1965, 1969), to account for this striking difference in the number of species on islands and adjacent mainland. If, on Fig. 2, the vertical distance between the mainland and island lines (drawn in) were constant then the mainland counts would merely be multiples of island counts for equal sized areas. This would result if a mainland area  $M$ , with  $n$  times the number of species as an island area  $I$  of equal size, had each of its component 10 acres (0.04 km<sup>2</sup>) with  $n$  times as many species as each component 10 acres of  $I$ . In this case, the explanation of island diversity is local. Once the reason for the decrease in diversity in 10 acres on  $I$  is found, nothing else needs to be known to explain why the island avifauna is depauperate. In MacArthur's phrase, the 'within habitat diversity' alone is responsible for the small size of the island avifauna.

A second alternative is that  $M$  still has  $n$  times the number of species that  $I$  has, but the 10 acre plots on  $M$  and  $I$  have the same number of species. That is, the mainland line has a greater slope than the island line, so that the explanation for the difference cannot be local. The component of 'between habitat diversity' is low on the island, and this is responsible for the impoverished island avifauna.

The first explanation is clearly incorrect. A line (not drawn in) joining points 50-51-52-54 (Creswick area, Victoria) in Fig. 2 is not a constant vertical distance above a line joining points 29, 30 or 31-32-33-38 (Tasmania). In Tasmania, once an area of the size of No. 33 is reached,



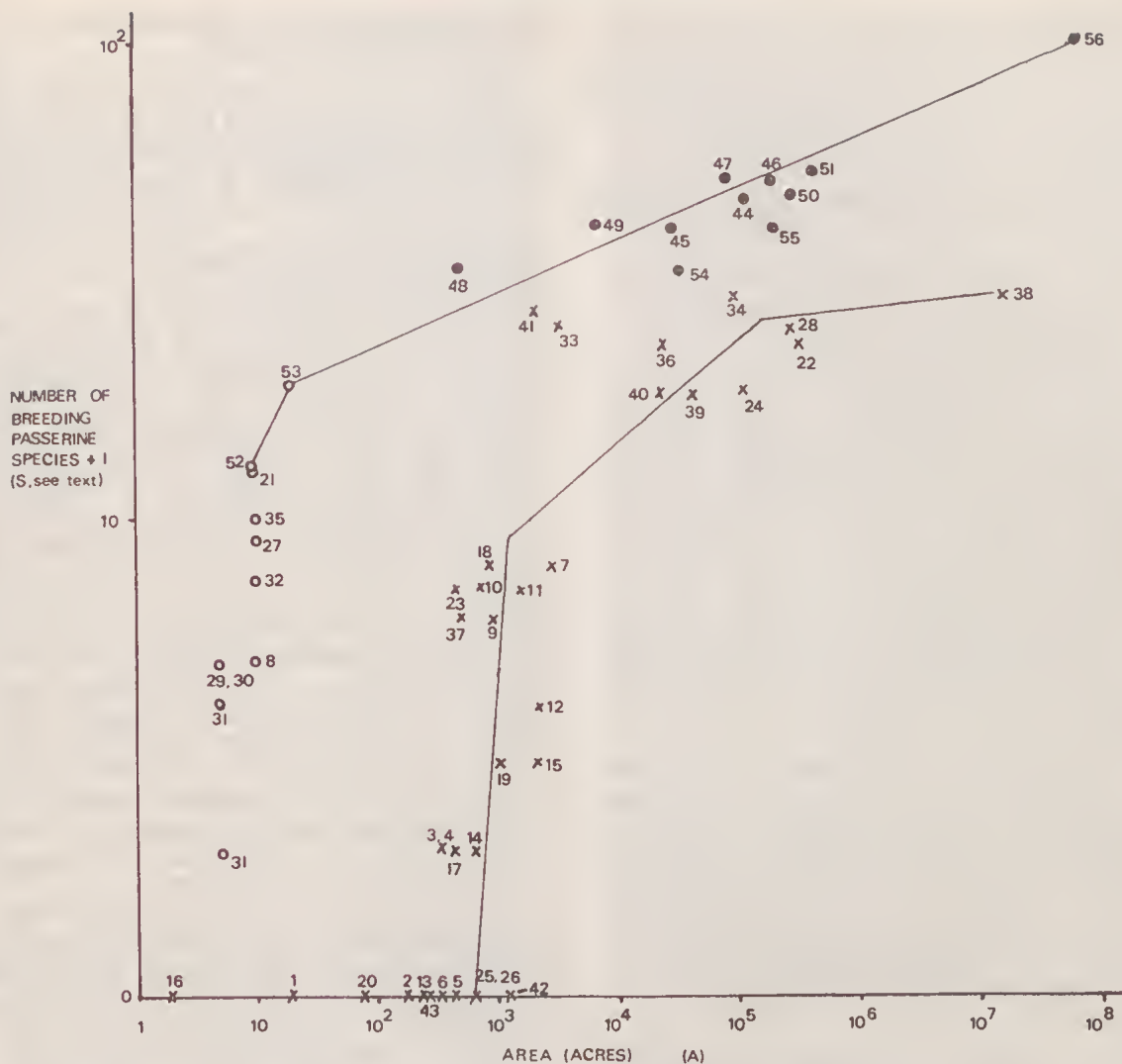


FIG. 2—The number of breeding passerine species (+1) plotted against the area in acres for island and mainland areas. X denotes islands; O censused plot; and ● mainland area.

almost all of the passerine species in Tasmania have been recorded. This probably also applies to extending 10 acre plots on Deal, King and Flinders Islands (Fig. 2). Once an area of about 100-1000 acres (0.4-4.0 km<sup>2</sup>) has been sampled on an island, not many more new species are likely to be recorded as breeding because most of the available habitats will have been covered. On the mainland, increasing the area adds more habitat types, resulting in many new species being recorded. Thus, although 10 acres (0.04 km<sup>2</sup>) on the mainland and Flinders Island support the same number of species, a mainland area of the same size as Flinders Island supports about twice as many species (Fig. 2). Similarly, 10 acres (0.04 km<sup>2</sup>) at Creswick supports about twice as

many species as 10 acres in Tasmania, but an area in Victoria of the size of Tasmania would contain nearly three times the number of species (Fig. 2).

MacArthur (1969) plotted numbers of species in tropical and temperate areas against area, and found that the tropical line rises more quickly for large areas (> 260 km<sup>2</sup>) than does the temperate line, so paralleling the result for mainland and island lines in Fig. 2. He concluded this meant tropical bird species have rather more finely subdivided their habitat relative to temperate species. This, however, may be more of an effect than a cause. Tropical areas have a great diversity of insect and plant species and hence of habitat types, which might cause bird species to show

narrow habitat preferences. An analogous explanation might apply to mainland and island areas. Another factor which is probably of importance on mainlands is that species there can be rarer without becoming permanently extinct, as can happen on islands. On the mainland, any extinction of a species in an area can be made good by continual re-invasion from surrounding habitats.

This last idea is well exemplified by comparing small islands which have no species with 10 acre (0.04 km<sup>2</sup>) plots on larger islands. A 10 acre plot on Clifty Island or the Monocoeur Islands has no species of birds, whereas 10 acre plots on Deal, King, Flinders or Maria Island, Tasmania, or Creswick will have up to about 13 species (Fig. 2). This discrepancy is easily explained, because Clifty Island and the Monocoeur Islands (as well as most of the islands smaller than 4 km<sup>2</sup>) have no *Eucalyptus* habitats for bird species to live and breed in. However, an island such as Rodondo, which is small but well vegetated with *Eucalyptus* and *Melaleuca* forest, has (probably) only one species breeding. Yet it has a planar area 29 times that of a 10 acre plot on the islands mentioned above.

This suggests that a 290 acre (1.17 km<sup>2</sup>) island, no matter how well vegetated, runs down with time. By virtue of its isolation, once it loses a species it is unlikely to regain it (or another). On the other hand, a 10 acre plot on a larger island is rather like a sample of the surrounding hospitable habitat. Any extinctions in a 10 acre plot are only temporary because they can be made good by invasion from the surrounding habitat.

Hence possibly for the species studied here, immigration and invasion rates onto islands are very low. On this hypothesis, many species are absent from the suitably vegetated Bass Strait islands because they cannot cross stretches of water sufficiently often or in numbers large enough to produce a viable population, and not because of ecological deficiencies on any islands. The best proof of this comes when species are deliberately introduced by man. This has not yet been done for any of the passerines studied here. However, it has been done with the Kookaburra (*Dacelo novaeguinae*) and Lyrebird (*Menura novaehollandiae*) into Tasmania (Abbott 1972 for details), and the Eastern Rosella (*Platycercus eximius*) onto Maria Island (J. H. Hemsley, pers. comm.). Such introductions have been successful because they remove the accidental nature of most movement of land bird species across stretches of water.

## DISTRIBUTION AND ABUNDANCE OF LAND BIRD SPECIES

The pattern of the distribution of land bird species among the islands of Bass Strait and Tasmania and nearby Southern Victoria is markedly similar to that obtained for Amphibia (Littlejohn and Martin 1965) and Reptilia (Rawlinson 1967). Ornithologists (e.g. Lack 1970) have thought that the ability of birds to fly gives them exceptional powers of distribution.

Data on the distribution and abundance of bird species has been derived from Wheeler (1967) and from personal observations for Southern Victoria, from Green (1969), Green and McGarvie (1971) and personal observations for the Bass Strait islands, and from Sharland (1958) and personal observation for Tasmania. These are summarized in Appendix Tables 1 A-D. Because Tasmania has been well watched ornithologically for over a century, the literature was searched to see how often Victorian land bird species not today found breeding on the islands and Tasmania have been recorded from there. Standard authorities consulted were Gould (1848), Ewing (1842, 1855), Legge (1887, 1902), Campbell (1900), North (1901-1914), Littler (1910), Sharland (1958) and Newman (1971), as well as the *Tasmanian Journal of Natural Science* 1842-1849, *Papers and Proceedings of the Royal Society of Tasmania* 1851—present, and *Ennu seriatim* (1901 onwards).

The distribution of species in Appendix Tables 1C and D falls into a relief pattern, suggesting an original widespread distribution of these species over Tasmania (s.l.), followed by differential extinction on all or some of the islands. Similar patterns exist for Amphibia (Littlejohn and Martin 1965), Reptilia (Rawlinson 1967), Mammalia (Hope 1969) and species of *Eucalyptus* (Abbott, unpubl. notes). On the other hand, 24 species of Southern Victorian land birds are unknown on the Bass Strait islands and Tasmania (Appendix Table 1E). Another 19 species are rarely recorded from these islands, except three that regularly breed on King Island (Appendix Table 1F). Eight other species, which are only vagrant to Southern Victoria, have been noted less than five times for Tasmania. Only one of these has been noted on the Bass Strait islands (Appendix Table 1G).

These distributional facts can be explained most simply by assuming these 51 species were not present in Southern Victoria when the Bass Strait landlink was last present. In the biogeographical studies of amphibians and reptiles cited above, species that today are found in Southern Victoria



but not in Tasmania and the Bass Strait islands have been called 'postglacial intrusives'. That is, the climatic conditions on the mainland at the time of isolation of these islands has largely determined which species were present on the islands (cf. Main 1961). This concept explains very well the distribution patterns summarized in Appendix Tables 1E-G.

It cannot be doubted that islands are not perfectly isolated from mainland areas, in the sense that there is movement of some species to and from (Appendix Tables 1F and G). This fact raises the question of why such species do not establish themselves. Lack (1971) stressed that birds wander more widely and more often than previously thought and that arrivals to islands are excluded by superior competitors already present. He writes '... any arrival [to a remote island] must compete immediately with the established species, and if it fails dies out' (Lack 1971:60; cf. Lack 1969:48). While it is true that most colonizing episodes do fail, it is not necessary to invoke competitive exclusion to explain why the arrivals do not establish themselves. Movement of most land birds across stretches of water is spasmodic and casual (as exemplified by evidence in Appendix Tables 1F and G), so that too few individuals of a species arrive at any one place or time on an island. Any invasion, to be successful, must involve at least one male and one female which must stay on the island and meet in the breeding season. Even species that migrate from northern Australia to Victoria in Spring have only rarely been recorded from the Bass Strait islands and Tasmania (Appendix Table 1F). Indeed, there are still many species that have not been recorded from Tasmania after 100 years of watching (Appendix Table 1E).

Conversely, if any of the 13 species endemic to the Tasmanian region have strayed in significant numbers to Southern Victoria (which is well watched by ornithologists), there should be records for these in the literature. Yet, only two (unconfirmed) sight records are known. These are *Anthochaera paradoxa*, one bird, recorded at Somers, 1951 (Reid 1967) and *Strepera fuliginosa*, one bird, at Orbost (Wakefield 1958b). Records of doubtful authenticity for two other species are discussed by Wakefield (1958a). These records are another successful test of the hypothesis of just how slight over-water movement of most land birds is.

Apparently suitable habitat exists on Tasmania and the large Bass Strait islands for most of the species listed in Appendix Tables 1E and F. Carefully managed introduction of these species

onto the islands should establish the species, as happened for the Kookaburra and Lyrebird in Tasmania, and the Eastern Rosella on Maria Island.

A simple model accounting for the distribution patterns of land bird species on the Bass Strait islands and Tasmania can now be sketched. Twelve species are members of double or triple invasions and double colonizations (Appendix Tables 1A and B), and have evolved through the make-and-break connexions across Bass Strait as sealevel fell and rose throughout the Pleistocene. If during the make-connexions *Eucalyptus/Acacia* vegetation covered Bass Strait, there would have been no physical barrier to movement of bird populations along the Tasmanian peninsula, although climatic effects could have affected any movement. Probably the avifaunas of Tasmania and Southern Victoria at these times intermixed. At the close of the last glacial, the species listed in Appendix Tables 1A-D became isolated on Tasmania, the Bass Strait islands, and Victoria. In some cases, extinction of some or all island populations followed, or surviving populations became subspecifically distinct (Abbott, unpubl.) as a result of reduction of any large scale movements between surviving populations. Since the landlink was last broken, and following mainland climatic changes, many land species (Appendix Tables 1E-G) moved into Southern Victoria, but were prevented from moving south by Bass Strait.

Although this scheme is admittedly speculative in parts, it should serve as a tentative framework in which to make finer analyses of the evolution of the avifaunas of the Bass Strait region.

#### FEEDING ECOLOGY OF SOME PASSERINE SPECIES

Currently, there are two views as to why island birds tend to undergo shifts in feeding zones and changes in feeding behaviour relative to their mainland representatives. First, following from an assumed general impoverishment of islands, shortage or unavailability of food may force many species to forage more widely. Such species differ from mainland equivalent species in where and how they seek their food (Keast 1968, 1970; Lack 1971). These 'generalists' are in such situations more successful than 'specialist' species, and are usually regarded as responsible for the latter being absent or rare (Lack 1971). A second view notes that islands always have far less breeding species than the mainland, so that those species present on an island can capitalize on this by foraging more widely (Grant 1965, 1966a; Mac-

Arthur et al. 1972, but see Morse 1971). Grant (1965) has also suggested that changes in lengths of bill and tarsus may be linked with increased ecological versatility of island bird species. The relationship between morphology and feeding behaviour of some passerine species on the Bass Strait islands, Tasmania and mainland Victoria is hence now examined.

In Tables 4-8, details of the morphology (length of bill, tarsus, hallux and wing) of males of each species are given. This information was derived by measuring all relevant material held in Australian collections. Sample sizes from Victoria and Tasmania for *Acanthiza*, *Sericornis*, *Acanthornis*, *Melithreptus* and *Meliphaga* are generally very much larger than those used by Keast (1968, 1970). Differences in bill length and hallux length between populations of the same species were tested using t-tests for statistical significance where sample sizes were large enough. Feeding behaviour was determined by following many individuals and timing their feeding from bark and foliage with a stopwatch, in the following areas: Deal Island, *Eucalyptus nitida* scrub in Lighthouse Gully; Flinders Island, *Eucalyptus globulus* and *E. viminalis* forest, and *Melaleuca ericifolia*/*Acacia melanoxylon* forest in Smiths Gully; King Island, *Eucalyptus globulus*/*E. viminalis*/*Melaleuca ericifolia* forest near Raffertys Gully; and Tasmania, *Eucalyptus tasmanica*/*E. linearis* forest on eastern side of Mt Louis; and Maria Island, *Eucalyptus obliqua*/*E. globulus* forest NE. of farm near Chinamans Bay. These feeding data have been grouped into categories, such as time spent foraging from bark and time spent gleaning leaves. I have used Keast's (1968, 1970) figures of foraging zonation for Victoria and Tasmania. Keast did not visit the Bass Strait islands, so that my data for three Bass Strait islands should also complement Keast's analysis of the Victorian and Tasmanian situation. In the Tables, I have included foraging data for Maria Island, although I have no morphological data for populations there.

These data are used here to test theories that have been proposed for the Tasmanian (Keast 1968, 1970) and other avifaunas (Grant 1968). Islands, for this purpose, can be treated as natural replicates where the relationship between feeding behaviour, morphology, and presence (or absence) of competitor species can be tested.

#### *Acanthiza ewingi* and *pusilla* (Table 4A, B)

The distribution and abundance of these *Acanthiza* species on the islands and Victoria have been summarized in Appendix Table 1A. *A.*

*pusilla* and *A. ewingi* live together on only two islands, namely King Island and Tasmania. *A. pusilla* is found alone on Deal Island (as well as Victoria), and *A. ewingi* alone on Flinders Island and Maria Island. On Tasmania, the species are well separated by habitat, with *A. pusilla* in drier habitats, and *A. ewingi* in gullies (Campbell 1905; Ridpath and Morcau 1966; pers. obs.). In Smiths Gully, Flinders Island, *A. ewingi* is very common in the vegetation lining the creek, but only vagrant individuals are found in the *Eucalyptus* forests on the slopes (pers. obs.). Near Raffertys Gully, King Island, *A. ewingi* is similarly most common close to the creek, and rare away from it (pers. obs.). On King Island, *A. pusilla* (of which only four specimens are known to exist, despite collecting in 1887, 1902, 1908, 1935, 1965 and 1968) was not observed during my stay there. However, Campbell (1903), who collected three of these specimens, reported it inhabiting 'the shorter scrub . . . away from the watercourses'. *A. pusilla* on Deal Island was common throughout the scrub and as there is little development of gully vegetation on the island, it is not surprising *A. ewingi* is absent. On mainland Victoria, *A. pusilla* is common in wet and dry forest (pers. obs.). These data show there is no consistent trend in habitat occupation between the two species in the different situations. Yet, current theory suggests species should expand their habitat when competitor species are absent (MacArthur and Wilson 1967). This was not observed.

When either *A. ewingi* or *A. pusilla* lives without the other, it is also predicted by current theory (e.g. Lack 1970, MacArthur and Wilson 1967) that their morphology and feeding behaviour should change. When *A. ewingi* is alone, it is predicted that bill and tarsal lengths will be different, as will feeding, from when *A. pusilla* is present. However, no significant differences between bill lengths and tarsal lengths were found between the Flinders Island and King Island populations of *A. ewingi*, although there is a highly significant difference in foraging zonation (Table 4B). The barkfeeding component in the ecology of *A. ewingi* on King Island is only minute, and yet *A. pusilla* there is exceedingly rare. The very long bill of *A. pusilla* on King Island suggests that it is an adaptation for probing bark. Green and McGarvie (1971) have suggested that on King Island *A. ewingi* is supplanting *A. pusilla*, and they have documented that *A. ewingi* today on King Island is more common than it was in 1887 and 1902. Although their explanation involving competitive exclusion seems



so plausible, my data (Table 4B) on the foraging of *A. ewingi* on King Island show that it does not feed from bark, which is where *A. pusilla* would be expected to feed. There are no records in the literature describing how *A. pusilla* on King Island feeds; but Keast (1970) has shown that the moderately longbilled *A. pusilla* in Tasmania has a strong barkprobing component in its feeding ecology. Thus, the existing data do not strongly support Green and McGarvie's hypothesis.

Although the bill length of *A. ewingi* on King and Flinders Island is intermediate between *A. ewingi* in Tasmania or *A. pusilla* in Victoria and *A. pusilla* in Tasmania, their feeding ecology as I have measured it is certainly not intermediate (Table 4). The plant species (*Eucalyptus*, *Melaleuca*) on which *Acanthiza* largely foraged are present on King and Flinders Islands, so there is no question of their habitat types differing between these islands.

Grant (1966b) has suggested that a long tarsus is mechanically useful to birds that use firm perches, such as thick branches, tree trunks, or the ground; and that a short tarsus is more advantageous when nonrigid (narrow) perches are used. On his hypothesis, individuals belonging to *A. ewingi* should more often forage on or near the ground or on the lower parts of trees, whereas *A. pusilla* should forage most often in the treetops (Table 4A). Also, *A. ewingi* on King and Flinders Islands should forage by gleaning leaves, whereas *A. ewingi* on Tasmania should be more of a barkprober (Table 4A). These predictions are falsified by data in Table 4B. More precise predictions can be made, as follow:

Because there is no significant difference in tarsal lengths between the King and Flinders Island populations of *A. ewingi*, there should be no difference in foraging zones. (False.)

Because there is no significant difference in tarsal lengths of *A. pusilla* in Tasmania and Victoria, there should be no difference in foraging zones. (False.)

Because *A. ewingi* on Tasmania has a significantly longer tarsus than *A. pusilla* on Tasmania or Victoria, it should feed from bark more than it does from foliage. This is true relative to *A. pusilla* in Victoria, but not so relative to *A. pusilla* in Tasmania.

There is thus no trend either way. Grant (1965) has also proposed that the longer bills and legs of island birds enhance their ecological versatility. In terms of the way I have measured feeding zonation, a completely versatile species should spend 50% of its feeding time probing bark, and 50% gleaning leaves and outerbranchlets for

food. The only populations of *Acanthiza* that remotely approach this condition are those of *A. pusilla* on Deal Island and Tasmania (Table 4B). However, time spent in feeding in each category for these islands is significantly different ( $X^2$  test, 1 df).

*Meliphaga flavicollis* and *leucotis* (Table 5A, B)

*M. flavicollis* is the island representative (Table 1) of the mainland *M. leucotis*. The bill lengths (Table 5A) of *M. flavicollis* on King and Flinders Island and Tasmania are not significantly different, but each is significantly different from that of the Victorian *M. leucotis*. As expected, the island populations, with one inexplicable exception, spend more time feeding from bark. Although the bill lengths of *M. flavicollis* on King and Flinders Islands are not significantly different, the King Island population spends a disproportionate amount of its time feeding from bark (Table 5B). No reason can be suggested that might explain such a difference. The chief bark probing species on the mainland (treecreepers *Climacteris* spp. and sitellas *Neositta* spp.) are absent from the whole of the Tasmanian region, so this cannot explain the difference. The change cannot easily be attributed to differences in tarsal length, as hypotheses of Grant (1966b) and Keast (1968) might suggest. The King and Flinders Island populations do not significantly differ in tarsal length, and the other two populations are significantly different from these. That is, the order of tarsal length is Tasmania (largest); King and Flinders Islands; and Victoria (smallest). If tarsal length were the cause of differences in foraging among the populations, then these should feed from bark in the same order. This is clearly not so (Table 5B). If the island populations are ecologically more versatile than the mainland population, the proportion of feeding time allotted to the three categories should be more nearly equal, namely around 30%. This is not so for any population (Table 5B).

*Melithreptus affinis* and *lunatus* (Table 6A, B)

The islands on which these members of a superspecies are found are set out in Appendix Table 1A. Apparently, no specimens have been collected from Deal Island, but the species is rare there and I was unable to observe it enough to measure its foraging behaviour. (For the record, the 60 seconds that I watched it feeding were spent gleaning foliage and the outerbranchlets of *Eucalyptus*). The samples of *M. affinis* (Table 6A) from Flinders and King Islands are too small to treat statistically. However, the Victorian population has a significantly longer bill,

and a significantly shorter tarsus and hallux than the Tasmanian population. Foraging data for these populations (Keast 1968) show scarcely any difference, though *M. affinis* where I studied it in Tasmania spent over 30% of its foraging time probing bark (Table 6B). The island populations are somewhat more versatile than the mainland population (Table 6B), thus agreeing with the hypothesis of ecological release.

*Melithreptus validirostris* and *gularis*  
(Table 7A, B)

*M. gularis* is only a vagrant south of the Great Dividing Range in Victoria (one record, Lower Glenelg 1958 (Learmonth 1966)); occasional records, You Yangs (Hore-Lacy 1959); one record, Somers (A. Reid pers. comm.); National Museum skins (one each) from Rockbank 1913, Chiltern 1900, Mt Macedon 1957; recorded at Bambra, c. 1900 (Hill 1903)). In contrast, *M. validirostris* is extremely abundant in *Eucalyptus* forest on King and Flinders Islands (pers. obs.) and Tasmania (Keast 1968; pers. obs.).

Because *M. validirostris* on the islands has a significantly longer tarsus and hallux than the mainland *M. gularis* (Table 7A), it would be expected to spend more of its time feeding from bark. This is confirmed by data in Table 7B. However it is not really more versatile in its feeding, because on King and Flinders Islands *M. validirostris* spends a disproportionate amount of its time feeding on bark. There is a real shift to feeding in almost a totally different zone on the islands (Table 7B), and not just diversification, as Keast (1968) incorrectly emphasized. Moreover, the King Island population of *M. validirostris* is significantly longer billed than the Tasmanian population, but is less versatile ecologically (Table 7B).

*Acanthornis magnus*, *Sericornis frontalis* and *humilis*  
(Table 8A)

This, and the next case, are examples of species that differ significantly in morphology from isolate to isolate, but show scarcely any difference in foraging zonation. *Acanthornis* is sometimes treated as a species of *Sericornis* (e.g. Keast 1970). The distribution of the three species is outlined in Appendix Table 1A. *Sericornis frontalis* and *humilis* spend over 95% of their foraging time on the ground or within 2 m of the ground on islands and mainland. No times were recorded because *Sericornis* rarely feeds anywhere else (pers. obs.; R. Wheeler, pers. comm.). In my experience, *Sericornis* leaves this low zone only when disturbed by the observer. Yet, real differences in bill and tarsal length do exist (Table

8A). The Tasmanian population has the largest bill, though it is not significantly different from that of the Flinders Island population. The bill length of the Victorian population is significantly less than that for any other population. Also, the King Island and Tasmanian populations have larger tarsi than the Deal and Flinders Island populations. *Sericornis* in Victoria has a tarsal length significantly less than that of any other population, but shows no tendency to feed above the ground. Presumably there is some subtle ecological factor on the ground that is responsible for the morphological differences found.

*Malurus cyaneus* (Table 8B)

The King Island, Flinders Island and Tasmanian populations are significantly different in bill length and tarsal length from the mainland (Victorian) one. However, *Malurus* is primarily a ground feeder (pers. obs.), and shows no difference in foraging zonation on the islands. Populations with smaller tarsi (Victoria, smallest, and Tasmania) do not show a perceptible trend to feed away from the ground. Thus morphological differences do exist, but it is not possible to correlate them with any differences in foraging heights, or preferences for feeding from bark versus leaves, or increased variability of feeding heights. Ants predominate in the stomachs of *Malurus cyaneus* that have so far been collected on the mainland (Rowley 1965, p. 297) and King Island (Green and McGarvic, 1971, p. 40). However, any difference in size of ants on mainland and island is yet to be looked for.

This analysis of the feeding ecology of 11 species of passerines does not support current hypotheses concerning the inter-relationships of morphology, feeding stations, habitat occupation and competition. According to the theory of 'ecological release', bird species on species-poor islands should expand their feeding zones relative to the feeding zones of the same or similar species on mainlands. On Tasmania and the Bass Strait islands, the opportunity for such ecological broadening exists because of the numerical impoverishment of bird species or of the poor variety of habitats.

The numbers of breeding passerine species in Southern Victoria, Tasmania, Maria Island, King Island, Flinders Island and Deal Island are respectively 78, 47, 36, 37, 34 and 12. The numbers of *Eucalyptus* species (dominating the forest habitats on these islands) are respectively 32, 24, 6, 3, 5 and 1.

With the most comprehensive example (*Acanthiza*), for which there are seven populations available for consideration, there was no evidence



that either species occupied broader habitats when its competitor was absent. The evidence also showed there was no broadening of foraging zones of *A. ewingi* on King Island and Maria Island, but *A. pusilla* on Deal Island did exhibit wider choice in where it fed. No consistent correlation between bill and leg dimensions and feeding ecology was found.

With *Meliphaga leucotis* and *flavicollis*, the King and Flinders Island populations foraged more at bark than did the mainland *M. leucotis*, but did not broaden in their choice between feeding at bark or leaves. Populations of the *Melithreptus lunatus* superspecies were found to broaden their foraging zones only slightly, and on Tasmania and Maria Island foraging was most generalized. *M. validirostris* on islands switched its foraging zone to probing bark, while the mainland *M. gularis* chiefly gleaned leaves. The island populations showed little broadening in feeding zonation.

In spite of differences in length of bill and tarsus, island populations of *Sericornis* species fed chiefly on the ground, which is where mainland populations forage. There was no tendency for the populations on the island to forage from bark. Similar conclusions apply to *Malurus cyaneus*.

These data allow three conclusions. First, it is not possible to consistently correlate morphological traits of populations with their foraging traits, nor morphological differences between island populations with foraging differences. Second, there was little evidence that island populations are more versatile in their choice of foraging zones than mainland ones. Keast's (1968) hypothesis that the absence of mainland bark-probing bird species from Tasmania is responsible for some *Melithreptus*, *Acanthiza* and *Meliphaga* species there switching to exploit this niche seems only partially true. The Bass Strait islands also lack the mainland bark-probing species, but the percentage of time the *Melithreptus*, *Acanthiza* and *Meliphaga* species spend feeding from bark differs markedly between islands. This suggests that differences in availability and/or abundance of food supply within islands, rather than ecological release, are important.

These conclusions can be further tested by studying the foraging of passerine species over the whole year. They may also be extended by stomach analyses.

#### VARIATION IN BILL AND TARSAL LENGTHS OF PASSERINES

Grant (1971), assuming that intraspecific variation in tarsal and bill length is adaptive, raised the

question of whether morphological variation in island populations should be any different from that in mainland populations. Several theories have been advanced suggesting that there should be a difference, although each theory suggests a conflicting result. First, if the diversity of habitats and food types on islands is less than on the mainland (as is widely assumed, e.g. by MacArthur 1965, Grant 1968, Keast 1970), morphological variation should be reduced on islands. In contrast (Grant 1966a), islands almost always have a decreased diversity of competitor species (with similar diets) and predator species, so that a larger range of food sizes should be available. Selection would therefore deal more kindly with extremes than on the mainland. Thus, island species may be expected to show increased morphological variation. However, it may also be possible (M. Littlejohn, pers. comm.) that the species present in the low number of habitats on the island simply utilize the food made available by the absence of competitor species, and in this case no morphological differences would be evident.

Extensive series of museum material collected from the Bass Strait islands, Tasmania and Victoria are suitable for looking critically at these ideas. As already mentioned, the history of the Bass Strait region suggests that the populations on the islands are relict ones, thus ruling out any influence Founder effect might have in determining variability (see Power, 1971, who had to contend with this factor). An analysis of the variation in bill length and tarsal length among samples of *Malurus cyaneus*, *Sericornis frontalis* and *S. humilis*, *Acanthiza ewingi* and *A. pusilla*, *Meliphaga leucotis* and *M. flavicollis*, *Melithreptus lunatus* and *M. affinis*, and *M. gularis* and *M. validirostris* is presented in Appendix Tables 2A and B. Samples are compared using the ratio of squared coefficients of variation, and the significance of differences is tested by the variance-ratio test. Lewontin (1966) has shown that the variance of logarithms of measurements is a measure of variability which does not change multiplicatively, and that an approximation to this measure is the squared coefficient of variation  $(s/\bar{x})^2$ . Most of my sample sizes are relatively large compared with Grant's (1971), nearly all of whose sample sizes range from 5-10.

Of the 46 statistical comparisons made of bill length variability, only 6 cases gave significant differences between mainland and island samples (Appendix Table 2A). It is to be expected that, due to chance, about 5% of these 46 comparisons would be significantly different. However, a  $X^2$

test of the null hypothesis confirms there is no real difference in variability of bill lengths between islands and mainland (Table 9A). The island populations were more variable than the mainland populations in 5 out of the 6 instances of significant differences. Numbers are too small to allow this to be tested statistically. Forty-six comparisons of variability of tarsal lengths were also made between island and mainland populations. Of these, 14 gave significant differences between samples. A  $X^2$  test for a 1:1 hypothesis shows that this difference is significant (Table 9B). That is, there is no real difference in variability in tarsal lengths between island and mainland populations (Table 9B). In four of the 14 significant cases the island population has the more variable tarsal length. A test of the significance of this is shown in Table 9C.

It is concluded from these data that the hypothesis of no real differences in variability of bill and tarsal lengths between island and mainland populations should be accepted. This supports the conclusions of similar analyses published by Grant (1967, 1971). There is, however, one important caveat in this type of analysis, pointed out by Van Valen (1965). He argued that when a mainland sample was gathered over a larger area than the island area, the variability of the mainland sample would increase such that many comparisons between island and mainland samples would be (erroneously) deemed nonsignificant. This seems a valid objection, since King and Flinders Island samples have been gathered over a much smaller area than has the Victorian sample (Abbott 1972, Appendix 3). However, the strength of the objection can be tested by comparing variabilities between Victorian and Tasmanian samples. These have been gathered over approximately the same sized area (see maps in Abbott 1972). Twelve comparisons are possible each for bill length and tarsal length variability. Comparisons were made by counting the number of cases in which the Victorian sample had the greater  $CV^2$ , and the results were tested by the  $X^2$  method (Table 9 D, E). No significant difference in variability between the Victorian and Tasmanian samples was found.

Two current hypotheses (the 'niche-variation' model of Van Valen and Grant, and that of Soule and Stewart (1970)), attempt to explain why island populations should show a higher variability in phenetic characters than mainland populations. The niche-variation model states that individuals of a species in a region with great variety of resources and habitats will have narrow niches, and the population will exhibit low vari-

ability in, for example, bill and tarsal lengths. In particular, species on islands and in temperate areas should show increased variation relative to species on mainlands or in the tropics. Soule and Stewart (1970) postulated instead that any increased variability in island populations is the result of a transient release of variation, possibly due to a breakdown in canalization, rare phenotypes having a selective advantage, or to occasional arrivals of mainland individuals onto islands.

My analysis tests whether there should be any change in variabilities between islands and mainland areas. It does not uphold the hypothesis that island populations do have more variable bills and tarsi. Willson (1969) tested whether temperate species have more variable bill dimensions than did tropical species, and found no tendency for temperate species to be more variable.

Grant (1971) argued that the Van Valen-Grant model could be tested by seeing how the foraging behaviour of species showing inter-regional differences in variability of tarsal length compared. As shown before (Table 4B), *Acanthiza ewingi* on King and Flinders Islands have very different foraging behaviours, yet they show no significant difference in variability of tarsal lengths (males or females, Appendix Table 2B). Comparison of the data in Tables 4-8 and Appendix Tables 2A and B shows the above example is not an isolated one. The Van Valen-Grant model is thus not supported by this study.

These results also bear on a question raised by Sheppard et al (1968), namely whether individual birds on islands expand their range of habitats, or whether each individual is as restricted as ever but more kinds of individuals are present. My data on tarsal and bill length variability do not support their second alternative.

Variability in bill and tarsal lengths could be determined selectively as follows. Selection could act on bill or tarsal length, on total body size, or on some other body part with which bill or tarsal length is correlated genetically (Grant 1971). For the species studied in this section, I tested to see whether bill or tarsal length were correlated with wing length (used as an indicator of body size). The significance of data are analysed in Table 10. Tarsal length is highly significantly correlated with wing length (Table 10B), but bill length is not significantly correlated with wing length (Table 10A). This suggests that if variation in wing length could be explained, most of the variation in tarsal length would automatically be explained. (However, Grant (1971) found the opposite for species from the Tres Marias Islands



and nearby Mexico). This is not an appropriate explanation for variation in bill length, so that one (or both) of the other modes of selection is (or are) responsible.

Neither of the predictions of the two theories outlined in the introduction of this section hold for the group of eleven passerine species studied here. This was unexpected, since the basic assumptions and arguments of these theories seem intuitively correct. The results of my analyses are, however, consistent with Littlejohn's suggestion (above). Other evidence from an analysis of variability of beak dimensions in finches on the Galapagos Islands (Abbott 1972 and unpubl.) similarly does not support either theory. These theories, in spite of their superficial attractiveness, need revising. This is in accord with other arguments put forward by Abbott (1972).

## CONCLUSIONS

1. An exposed Bass Strait during the last glacial may have been important in the evolution and ecology of the bird species which are today restricted to the Tasmanian region. Compared with other Australian continental islands, islands in the Tasmanian region have a high percentage (up to 17%) of their avifauna not found on mainland Australia. With the available data, it is not possible to sort out isolation by distance, and isolation during time, as explanatory factors.

2. Numbers of forest passerine species on the Bass Strait islands and Tasmania when plotted against their area do not satisfactorily fit the standard exponential species/area curve. Relative to mainland Victoria, these islands have a depauperate passerine component in their avifaunas.

3. When Bass Strait was last flooded, the islands so formed acted virtually as closed systems, in that many species so isolated have since become extinct and most mainland species have been unable to invade. The pattern of distribution of species is largely relict. Fifty-one species of land birds in Southern Victoria apart from three breeding on King Island are accidental or unknown from Tasmania and the Bass Strait islands. These are probably postglacial intrusives into Southern Victoria.

4. It is not necessary to invoke competitive exclusion to explain why Tasmania and the Bass Strait islands have species-poor avifaunas. Extralimital records of mainland species of land birds are scarce, and this is not entirely due to a lack of observers on the islands.

5. Quantitative data on the feeding ecology of eight passerine species indicate there is no

consistent correlation of beak and leg dimensions with time spent feeding from bark and leaves. There was little evidence for ecological release with relaxed competition on the Bass Strait islands and Tasmania.

6. No significant differences in variation in bill length and tarsal length were found for populations of eleven passerine species on the Bass Strait islands, Tasmania and Victoria. The generally accepted theory of competition would have predicted otherwise.

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TABLE 1  
DISTRIBUTION OF BIRD SPECIES ENDEMIC TO TASMANIA REGION

Species on Tasmania	On other islands
<i>Tribonyx mortierii</i> , Tasmanian native hen	King, Deal, Flinders, Cape Barren
<i>Platycercus caledonicus</i> , Green Rosella	King, Flinders, Cape Barren
<i>Acanthiza ewingi</i> , Ewing's Thornbill	King
<i>Acanthornis magnus</i> , Scrubtit	King, Flinders, Cape Barren
<i>Sericornis humilis</i> , Brown Scrubwren	King, Flinders, Cape Barren
<i>Petroica vittata</i> , Dusky Robin	King (?still), Flinders
<i>Pardalotus quadragintus</i> , Forty spotted Pardalote	King, Flinders, Cape Barren
<i>Melithreptus affinis</i> , Black headed Honeyeater	King, Flinders, Cape Barren
<i>M. validirostris</i> , Strong billed Honeyeater	King, Flinders, Cape Barren
<i>Meliphaga flavicollis</i> , Yellow throated Honeyeater	King, Flinders, Cape Barren
<i>Anthochaera paradoxa</i> , Yellow wattle bird	King
<i>Strepera arguta</i> , Clinking Currawong	King, Flinders, Cape Barren
<i>S. fuliginosa</i> , Black Currawong	King, Flinders, Cape Barren
Species endemic to islands alone (not on Tasmania)	
<i>Dromaius ater</i> , King Island Emu	King (extinct)

NOTES: 1. Information from Green (1969, 1971) and Green and McGarvie (1971), and personal observation on all islands excluding Cape Barren, for which Milledge (unpubl. lists) and Whinray (1970). 2. *Lathamus discolor*, Swift Parrot has been wrongly treated as endemic to Tasmania by past workers (Abbott and Milledge, in press).

TABLE 2  
PERCENTAGES OF TASMANIAN REGION ENDEMIC SPECIES ON  
TASMANIA AND BASS STRAIT ISLANDS  
(TOTAL NUMBER OF SPECIES ON EACH ISLAND IN PARENTHESES)

Group	Tasmania	King I.	Flinders I.	Cape Barren I.	Deal I.	Authority
Mimosaceae	11 (18)	0 (8)	0 (16)	0 (7)	0 (3)	J. H. Willis, unpubl. list; Curtis (1956); P. A. Barnett, unpubl. list.
Myrtaceae	33 (45)	0 (9)	0 (21)	0 (11)	0 (7)	Willis and Barnett
<i>Eucalyptus</i>	46 (24)	0 (3)	0 (5)	0 (5)	0 (1)	Willis and Barnett, Curtis (1956); Pryor and Johnson (1971)
Proteaceae	54 (24)	0 (2)	18 (11)	25 (8)	0 (1)	Willis, Barnett, Curtis (1967)
Epacridaceae	62 (72)	0 (10)	0 (21)	0 (11)	0 (5)	Willis, Barnett, Curtis (1963)
Mosquitoes	7 (30)	0 (10)	0 (22)	?	0 (3)	Dobrotworsky (1966)
Amphibians	20 (10)	0 (6)	0 (6)	?	0 (0)	Littlejohn and Martin (1965); Littlejohn (pers. comm.)
Reptiles	14 (14)	11 (9)	16 (12)	?	0 (6)	Rawlinson (1967) and pers. comm.; Green and McGarvie (1971)
Birds	12 (104)	17 (72)	12 (73)	13 (c.60)	6 (18)	see Table 1, note
Mammals	13 (31)	0 (14)	0 (18)	?	0 (2)	Hope (1969)



TABLE 3

## ENDEMIC BIRD SPECIES ON AUSTRALIAN ISLANDS

Island	Nearest mainland point(s)	Minimum distance km	Area km <sup>2</sup>	Height m	Approx. depth of Strait at which island separates from mainland (m)	When isolated (years BP)	Number of bird species not shared with mainland	Number of bird species restricted to island
King	Cape Otway, Vic.	89	1,100	210	72-81	16000	12 <sup>♂</sup>	1
*Deal	Wilson's Promontory Vic.	89	12	285	54-60	13000-14000	1	0
*Flinders	Wilson's Promontory Vic.	139	1,300	750	54-60	13000-14000	9	0
*Cape Barren	Wilson's Promontory Vic.	210	470	680	54-60	13000-14000	8	0
*Tasmania	Wilson's Promontory Vic.	240	62,000	1,590	54-60	13000-14000	13	2
Kangaroo	Capes Jervis and Spencer, S.A.	13,45	4,350	295	28-36	10000-11000	1 (extinct)	1
Rottneest	Fremantle, W.A.	18	19	39	9	6000-7000	0	0
Houtman Abrolhos	Geraldton, W.A.	57	10	15	36-45	11000-12000	0	0
Dirk Hartog	Edel Land, W.A.	3.2	640	182	7.5	6000	1 <sup>≠</sup>	0
Dorre	Carnarvon, W.A.	55	47	45	15	8000	0	0
Bernier	Carnarvon, W.A.	47	45	51	16	8000	0	0
Barrow	N.W. Australia	64	220	81	12	7000	1 <sup>≠</sup>	0
*Melville	Darwin area, N.T.	24	5,700	104	18-36	8000-11000	0	0
*Groote Eylandt	E. Arnhem Land, N.T.	42	2,500	210	18-21	8000-9000	0	0
*Torres Strait islands	Cape York, Qd	29-57	variable		9	6000-7000	0	0
Fraser	Inskip Point, Qd	< 2	1,600	235	0.3-9	<6000	0	0
Moreton	Brisbane area, Qd	23	160	275	< 12	<7000	0	0
*North Stradbroke	Brisbane area, Qd	5	320	215	0.3-1.5	<1000	0	0

\* with islands intervening

♂ one of these, and possibly another, now extinct (see notes, Table 1)

≠ endemic to Barrow and Dirk Hartog Islands

Source: See Appendix 1 in Abbott (1972)

TABLE 4A, B

A MORPHOLOGY OF *ACANTHIZA* SPECIES (means in mm).

<i>A. ewingi</i> ♂	Bill	Tarsus	Hallux	Wing	N
Tasmania	11.8	21.4	7.8	54.6	37
King Island	12.3	20.4	7.6	53.9	16
Flinders Island	12.4	20.6	7.8	52.2	9
<i>A. pusilla</i> ♂					
Tasmania	13.1	19.3	8.1	54.6	29
King Island	15.8	19.0	8.6	53.0	3
Deal Island	13.9	22.5	8.1	58	1 (live specimen)
Victoria	11.7	19.8	7.4	51.7	30

## B FEEDING ECOLOGY (%)

	<i>A. pusilla</i>				<i>A. ewingi</i>		
	Deal I.	Tasmania*	Victoria*	Tasmania*	King	Flinders I.	Maria I.
bark	65	41	11	16	0.5	21	4.5
outerbranchlets/ foliage	35	66	87	82	99.5	79	95.5
N	1040	1078	1265	598	2975	7689	440

\* From Keast (1970). His N = total no. feeding actions; My N = total no. seconds feeding.

TABLE 5A, B

A MORPHOLOGY OF *MELIPHAGA* SPECIES (♂, means in mm)

	Bill	Tarsus	Hallux	Wing	N
Victoria ( <i>M. leucotis</i> )	20.2	23.4	11.7	97.7	31
King Island ( <i>M. flavicollis</i> )	21.6	25.1	13.4	106.1	9
Flinders Island ( <i>M. flavicollis</i> )	21.7	24.6	13.2	105.1	8
Tasmania ( <i>M. flavicollis</i> )	21.5	25.6	13.6	106.1	50

## B FEEDING ECOLOGY (%)

	Victoria*	King I.	Flinders I.	Tasmania*	Tasmania	Maria I.
lower trunk	25	12	4	10	3	0
upper trunk and branches	10	61	47	36	29	56
outerbranchlets and foliage	65	28	49	55	71	44
N	1170	1625	533	1350	392	784

\* From Keast (1968). His N = total no. feeding actions; My N = total no. seconds feeding.

TABLE 6A, B

A MORPHOLOGY OF *MELITHREPTUS LUNATUS* SUPERSPECIES (♂, means in mm)

	Bill	Tarsus	Hallux	Wing	N
Victoria ( <i>M. lunatus</i> )	15.4	17.3	8.2	77.0	24
King Island ( <i>M. affinis</i> )	14.4	18.9	8.6	78.2	5
Flinders Island ( <i>M. affinis</i> )	15.0	19.0	9.0	76.0	3
Tasmania ( <i>M. affinis</i> )	15.0	19.1	8.9	78.5	44



## B FEEDING ECOLOGY (%)

	Victoria*	King I.	Flinders I.	Tasmania*	Tasmania	Maria I.
lower trunk and ground	0	0	0	0	7	2
flowers	0	12	2	0	4	0
upper trunk	0	0	2	0	0	5
branches	5	0	16	5	24	35
outerbranchlets and foliage	97	88	80	98	65	59
N	680	480	2628	1579	2118	1206

\* From Keast (1968). His N = total no. feeding actions; My N = total no. seconds feeding.

TABLE 7A, B

A MORPHOLOGY OF *MELITHREPTUS GULARIS* SUPERSPECIES (♂, means in mm)

	Bill	Tarsus	Hallux	Wing	N
Victoria ( <i>M. gularis</i> )	16.6	19.2	9.9	90.0	6
King Island ( <i>M. validirostris</i> )	21.5	20.3	11.0	83.7	11
Flinders Island ( <i>M. validirostris</i> )	20.7	19.7	10.5	80.7	3
Tasmania ( <i>M. validirostris</i> )	20.0	20.8	11.1	82.8	22

## B FEEDING ECOLOGY (%)

	Victoria*	King I.	Flinders I.	Tasmania*	Tasmania	Maria I.
lower trunk	2	95	29	5	45	0
upper trunk and branches	27	5	70	62	55	100
outerbranchlets and foliage	69	0	2	33	0	0
N	520	6965	7662	2250	595	98

\* From Keast (1968). His N = total no. feeding actions; My N = total no. seconds feeding.

TABLE 8A, B

A MORPHOLOGY OF *SERICORNIS* SPECIES AND *ACANTHORNIS MAGNUS* (means in mm)

	Bill	Tarsus	Hallux	Wing	N
Victoria (♂ <i>S. frontalis</i> )	14.7	21.5	9.1	58.7	31
King Island (♂ <i>S. humilis</i> )	16.2	24.2	10.3	62.1	20
Flinders Island (♂ <i>S. humilis</i> )	16.5	23.0	10.0	60.7	18
Deal Island (♂ <i>S. ?frontalis</i> )	16.3	22.9	10.1	61.6	10
Tasmania (♂ <i>S. humilis</i> )	16.7	24.7	10.5	63.1	43
Tasmania (unsexed <i>A. magnus</i> )	15.3	21.4	9.7	55.9	18
King Island (unsexed <i>A. magnus</i> )	15.6	20.3	9.3	53.6	5

B MORPHOLOGY OF *MALURUS CYANEUS* (♂, means in mm)

	Bill	Tarsus	Hallux	Wing	N
Victoria	9.0	22.3	8.1	52.4	54
King Island	9.9	24.0	8.7	54.9	28
Flinders Island	10.0	24.1	8.6	55.7	17
Tasmania	9.7	23.4	8.7	54.4	72

TABLE 9  
X<sup>2</sup> TESTS

	<i>No. instances</i>
A. Comparison of differences in variability of bill length between islands and mainland No significant difference Significant difference X <sup>2</sup> test of H <sub>0</sub> , P < 0.001	40 6
B. Comparison of differences of variability of tarsal length between islands and mainland No significant difference Significant difference X <sup>2</sup> test of H <sub>0</sub> , P < 0.01	32 14
C. Comparison of differences in direction of variability of tarsal length between islands and mainland Island lengths sig. less variable Island lengths sig. more variable X <sup>2</sup> test of H <sub>0</sub> , P > 0.10	10 4
D. Comparison of differences in variability of bill length between Victoria and Tasmania Variability of Victorian populations greater Variability of Tasmanian populations greater X <sup>2</sup> test of H <sub>0</sub> , P > 0.20	4 8
E. Comparison of differences in variability of tarsal length between Victoria and Tasmania Variability of Victorian populations greater Variability of Tasmanian populations greater X <sup>2</sup> test of H <sub>0</sub> , P > 0.50	7 5

TABLE 10  
X<sup>2</sup> TESTS

	<i>No. instances</i>
A. Comparison of significance of correlations between bill and wing lengths of 26 populations Significant correlation coefficient Nonsignificant r X <sup>2</sup> test of H <sub>0</sub> , P > 0.20	16 10
B. Comparisons of significance of correlations between tarsal and wing lengths of 26 populations Significant r Nonsignificant r X <sup>2</sup> test of H <sub>0</sub> , P < 0.001	23 3



## APPENDIX TABLE 1A-D

PATTERNS OF DISTRIBUTION AND ABUNDANCE OF BIRD SPECIES  
ON TASMANIA, BASS STRAIT ISLANDS, AND SOUTHERN VICTORIA

Species	Tasmania	King Island	Flinders Island	Deal Island	S. Victoria
A. Multiple invasions					
<u>Pardalotus quadragintus</u>	l.c	l.vr	l.r	-	-
<u>P. punctatus</u>	w.c	l.r	w.c	-	w.c
<u>Acanthiza ewingi</u>	w.a	w.a	w.a	-	-
<u>A. pusilla</u>	w.a	l.vr	-	w.a	w.a
<u>Acanthornis magnus</u>	w.c	l.r	-	-	-
<u>Sericornis humilis</u>	w.a	w.a	w.a	-	-
<u>S. frontalis</u>	-	-	-	w.a	w.a
<u>Melithreptus affinis</u>	w.a	l.r	w.a	-	-
<u>M. lunatus</u>	-	-	-	l.vr	w.a
<u>Platycercus caledonicus</u>	w.a	w.c	w.a	l.c	-
<u>P. elegans</u> *	-	-	-	-	w.a
B. Double colonization					
<u>Strepera fuliginosa</u>	w.a	w.c	w.a	-	-
<u>S. graculina</u>	-	-	-	-	w.a
<u>S. arguta</u>	w.a	-	-	-	-
<u>S. versicolor</u>	-	-	-	-	w.a
C. Species found in Tasmania and southern Victoria, but not on any Bass Strait island					
<u>Platycercus eximius</u>	l.c	-	-	-	w.c
<u>Cinclosoma punctatum</u>	w.c	-	-	-	w.a
<u>Acanthiza chrysorrhoa</u>	w.a	-	-	-	w.c
<u>Calamanthus fuliginosa</u>	w.c	-	-	-	l.c
<u>Stipiturus malachurus</u>	w.c	-	-	-	l.c
<u>Anthochaera chrysoptera</u>	l.c	-	-	-	l.c
<u>Manorhina melanocephala</u>	l.a	-	-	-	w.c
<u>Cracticus torquatus</u>	w.c	-	-	-	w.c
<u>Gymnorhina tibicen</u>	w.c	introduced	introduced	-	w.c
D. Species found in Tasmania and southern Victoria, and only some islands in Bass Strait (see also A above)					
<u>Malurus cyaneus</u>	w.a	w.c	w.c	-	w.a
<u>Petroica multicolor</u>	w.a	-	w.a	-	w.a
<u>Emblema bella</u>	l.c	-	l.c	w.c	w.c
<u>Phylidonyris novaehollandiae</u>	w.a	w.r	l.c	-	w.a

Notation for A-D: w = widespread; l = localized; - = absent; a = abundant  
c = common; r = rare; vr = very rare.

\* Platycercus elegans also found on Rodondo Island (Bechervaise 1947)

APPENDIX TABLE 1E  
SPECIES COMMON AND WIDESPREAD IN  
SOUTHERN VICTORIA, BUT NEVER RE-  
CORDED FROM TASMANIA OR BASS STRAIT  
ISLANDS

## Non-passerines

## PSITTACIDAE

*Glossopsitta porphyrocephala*, Purple crowned Lori-  
keet

*Alisterus scapularis*, King Parrot

## ALCEDINIDAE

*Dacelo novaeguinae*, Kookaburra (Before 1900, see  
text)

## Passerines

## MENURIDAE

*Menura novaehollandiae*, Lyrebird (Before 1934, see  
text)

## ACANTHIZIDAE

*Acanthiza lineata*, Striated Thornbill

*A. nana*, Little Thornbill

*Hylacola pyrrhopygia*, Chestnut tailed Groundwren

## MALURIDAE

*Dasyornis broadbenti*, Rufous Bristlebird

## MONARCHIDAE

*Seisura iniqueta*, Restless Flycatcher

## MUSCICAPIDAE

*Microeca leucophaea*, Jacky Winter

*Eopsaltria australis*, Yellow Robin

## FALCUNCULIDAE

*Falcunculus frontatus*, Shrike-tit

*Psophodes olivaceus*, Eastern Whipbird

## NEOSITTIDAE

*Neositta chrysoptera*, Sitella

## DICAEDIDAE

*Pardalotus ornatus*, Eastern Striated Pardalote

*Dicaeum hirundinaceum*, Mistletoe Bird

## MELIPHAGIDAE

*Meliphaga virescens*, Singing Honeyeater

*M. fusca*, Fuscous Honeyeater

*M. leucotis*, White eared Honeyeater

*M. melanops*, Yellow tufted Honeyeater

*M. penicillata*, White plumed Honeyeater

*Anthochaera carunculata*, Red Wattle Bird

## ESTRILDIDAE

*Aegintha temporalis*, Red browed Finch

## PTILONORHYNCHIDAE

*Ptilonorhynchus violaceus*, Satin Bower Bird

## APPENDIX TABLE 1F

SPECIES COMMON AND WIDESPREAD IN  
SOUTHERN VICTORIA, BUT ACCIDENTAL  
OR CASUAL TO TASMANIA AND BASS STRAIT  
ISLANDS, \*SPRING MIGRANTS TO SOUTHERN  
AUSTRALIA.

## Non-passerines

## PSITTACIDAE

*Trichoglossus haemotodus*, Rainbow Lorikeet

TASMANIA: Ewing (1842) queries a specimen from  
Swanport. Specimens shot 1871 (one near New Nor-

folk) and 1872 (Anon. 1872: 6, 50; 1873: 39), but  
no details. No further records (Sharland 1958, New-  
man 1971).

BASS STRAIT ISLANDS: No records, except for King  
Island (one bird, 1966) (Green and McGarvie  
1971).

*Glossopsitta pusilla*, Little Lorikeet

TASMANIA: Noted by Ewing (1842) for Maria Island,  
and by subsequent cataloguers. Possibly resident,  
though most reports are unconfirmed (Sharland  
1958).

BASS STRAIT ISLANDS: No records.

*Cacatua roseicapilla*, Galah

TASMANIA: First record, no details (Anon. 1881: 3).  
One pair, May 1908 (Littler 1910). Occasionally  
since (Sharland 1958, Newman 1971). Some aviary  
escapees (D. Milledge, pers. comm.).

BASS STRAIT ISLANDS: Odd birds occasionally on King  
and Flinders Islands (Green 1969, Green and Mc-  
Garvie 1971).

*Callocephalon fimbriatum*, Gang Gang Cockatoo

TASMANIA: First record, Circular Head (Ewing 1842);  
occasional visitor since (Anon. 1853: 143; Sharland  
1958).

KING ISLAND: Specimen collected 1802 (Stresemann  
1951); Other records (Anon. 1874: 50, Campbell  
1888, Anon. 1908: x, Green and McGarvie (1971)).  
Probably resident there (Littler 1910).

No records for other islands.

## ALCEDINIDAE

\**Halcyon australiasiae*, Sacred Kingfisher

TASMANIA: First record, Southport (Anon. 1870: 7,  
87). Also, Howrah (Anon. 1874: 9) and Cam-  
bridge (Anon. 1886: cxlvii). Occasional records since  
(Sharland 1958). No breeding records. Not regarded  
as vagrant by Milledge (unpubl. 1970).

KING ISLAND: Campbell (1888); Green and McGar-  
vie (1971).

DEAL ISLAND: Campbell (1891). No breeding records  
for these islands.

No records for Flinders Island.

## Passerines

## HIRUNDINIDAE

\**Petrochelidon ariel*, Fairy Martin

TASMANIA: First record, Bridport, about 1886, breed-  
ing (Wintle 1887, but see Littler 1910). Not listed  
by Legge (1902). One old nest, Tunbridge (Vincent  
1968); One bird, near Hobart, October 1971 (Vincent  
1972).

KING ISLAND: No records.

FLINDERS ISLAND: Recorded by Le Souef (1902),  
though probably in error for *P. nigricans* (Tree Mar-  
tin), which was not recorded.

## CAMPEPHAGIDAE

\**Lalage sueurii*, White winged Triller

TASMANIA: First listed (no details) by Campbell  
(1900) and Legge (1902), although Littler (1910)  
remarked, 'I am unable to discover how and when  
this bird first came to be placed on the Tasmanian  
list'. Subsequent records are Kelso, November 1912  
(Littler 1913 and West Devonport, November 1916  
(Dove 1917). Three birds near Devonport, November  
1969, of which one pair bred (Pinner and Bird 1970).  
KING ISLAND: Occasional (Green and McGarvie  
1971).

FLINDERS ISLAND: No records.



## SYLVIIDAE

*Cisticola exilis*, Tailor Bird

TASMANIA: First and only records, which are also breeding records, for Spring 1911-12 at Springfield (Fletcher 1913). These are discussed by Sharland (1972) and Courtney Haines (1972).

KING ISLAND: Breeding species (Campbell 1888, 1903; Green and McGarvie 1971).

No records for other islands.

## RHIPIDURIDAE

\**Rhipidura rufifrons*, Rufous Fantail

TASMANIA: First and only record (unconfirmed): one bird, Stanley, March 1945 (Sharland 1945).

No record for islands.

*Rhipidura leucophrys*, Willie Wagtail

TASMANIA: No published records.

KING ISLAND: Odd birds (Green and McGarvie 1971).

FLINDERS ISLAND: Odd birds (Green 1969; E. Warren pers. comm.).

## MONARCHIDAE

\**Myiagra rubecula*, Leaden Flycatcher

TASMANIA: First record Falmouth 1868 (Legge 1889); also Falmouth, February 1874 (Legge 1875). 'Regular visitor' (Littler 1910). Boat Harbour district (Fletcher 1918), though probably confused with *M. cyanoleuca* which was not listed. Unconfirmed sighting, November 1964 (Thomas 1965). First breeding record, January 1968 at Maria Island (Wall 1969).

KING ISLAND: no records.

FLINDERS ISLAND: Le Souef (1902), but not since.

## PACHYCEPHALIDAE

\**Pachycephala rufiventris*, Rufous Whistler

KING ISLAND: record occasionally (Green and McGarvie 1971).

No records for other islands.

## CLIMACTERIDAE

*Climacteris leucophaea*, White throated Treecreeper

TASMANIA: Unconfirmed sight records, Quamby Bluff (Legge 1904) and near Wilmot (Fletcher 1908). Specimens allegedly collected by R. Gunn (Legge 1904).

No records for islands.

## MELIPHAGIDAE

*Meliphaga novaehollandiae*, Yellow faced Honey-eater

KING ISLAND: Breeding species (M. McGarvie, pers. comm.). No other records.

*Melithreptus brevirostris*, Brown headed Honeyeater.

KING ISLAND: One specimen known (Mathews 1912; 394). Mathews took this specimen as representative of a King Island subspecies, an error which has been repeated by Cayley (1958) and Courtney (1963: 57).

**Editor's Note:** Since this table was compiled, the author informs me that he has seen the specimen on which this record is based and concludes that the bird must have been taken on Kangaroo Island not King Island (see Abbott's note in press, Emu Vol. 73).

## GRALLINIDAE

*Grallina cyanoleuca*, Peewee

TASMANIA: First record, one pair at Stanley, July 1888 (Anon. 1889; xxxli and North 1902: 89). Specimen collected at Spring Bay, April 1904 (Tas-

manian Museum). One bird near Triabunna, October 1969 (Milledge 1970). No breeding records (Sharland 1958).

KING ISLAND: Occasional (Green and McGarvie 1971).

FLINDERS ISLAND: Occasional (Green 1969; E. Warren, pers. comm.).

## ARTAMIDAE

\**Artamus personatus*, Masked Wood Swallow

\**A. superciliosus*, White browed Wood Swallow

KING ISLAND: Occasional, although *A. superciliosus* turns up each year. There are no breeding records (Green and McGarvie 1971).

There are no records for other islands.

## APPENDIX TABLE 1G

SPECIES ACCIDENTAL OR CASUAL TO  
TASMANIA WHICH ARE ALSO ACCIDENTAL  
OR CASUAL TO SOUTHERN VICTORIA.  
ALL BUT ONE HAVE NOT BEEN  
RECORDED FOR THE BASS STRAIT ISLANDS

## Non-passerines

## COLUMBIDAE

*Ptilinopus regina*, Red crowned Pigeon

TASMANIA: First record, Bothwell May 1922 (Lord and Arnold 1922). Also, Exeter, April 1968 (Green 1969). Individual birds only.

*Ptilinopus superbus*, Purple-crowned Pigeon.

TASMANIA: First record, Quamby about 1872 (Anon. 1873: 40). Also, Eddystone Point, April 1970 (Sharland 1970). Individual birds only.

*Lopholaimus antarcticus*, Topknot Pigeon

TASMANIA: First recorded by Ewing (1855). Also, N.E. coast, July 1907 (Littler 1910).

## PSITTACIDAE

*Nymphicus hollandicus*, Cockatiel

TASMANIA: First record at Riversdale, about 1884 (Anon. 1885: lxx). Three subsequent records (Sharland 1958).

## CUCULIDAE

*Scythrops novaehollandiae*, Channel billed Cuckoo

TASMANIA: First record, Clarence Plains about 1867 (Anon. 1868: 37). Also, near Launceston, February 1943 (Sharland 1943). Individual birds only.

## CORACIIDAE

*Eurystomus orientalis*, Dollar Bird

TASMANIA: First confirmed record, Mt Jukes, about 1918 (Lord 1918). No subsequent records.

## Passerines

## DICRURIDAE

*Dicrurus hottentotus*, Spangled Drongo

TASMANIA: First record, Falmouth, May 1888 (Legge 1889). Subsequent records at Stanley 1888 and Bridport 1900 (Sharland 1958).

## ARTAMIDAE

*Artamus leucorhynchus*, White breasted Wood Swallow

KING ISLAND: Occasional (Green and McGarvie 1971). No other records.

APPENDIX TABLE 2A

SIGNIFICANCE OF DIFFERENCES IN VARIATION IN BILL LENGTH BETWEEN ISLAND AND MAINLAND POPULATIONS. F VALUES ARE CALCULATED FROM SQUARED COEFFICIENTS OF VARIATION, AND THE LOCALITY WITH THE GREATER VARIANCE IS UNDERLINED

Species	Localities	F (df)	P
<u>Malurus cyaneus</u>	♂ <u>Victoria</u> x King Island	1.69 (51,27)	ns
	♂ <u>Victoria</u> x Flinders Island	1.28 (51,16)	ns
	♂ King Island x <u>Flinders Island</u>	1.32 (16,27)	ns
	♂ <u>Victoria</u> x <u>Tasmania</u>	1.04 (51,65)	ns
	♂ King Island x <u>Tasmania</u>	1.63 (65,27)	ns
	♂ Flinders Island x <u>Tasmania</u>	1.23 (65,16)	ns
<u>Sericornis frontalis/</u> <u>humilis</u>	♂ <u>Victoria</u> x King Island	1.19 (30,19)	ns
	♂ <u>Victoria</u> x Flinders Island	1.14 (30,16)	ns
	♂ King Island x <u>Flinders Island</u>	1.05 (16,19)	ns
	♂ <u>Victoria</u> x <u>Tasmania</u>	1.08 (30,38)	ns
	♂ King Island x <u>Tasmania</u>	1.10 (38,19)	ns
	♂ Flinders Island x <u>Tasmania</u>	1.05 (38,16)	ns
	♀ <u>Victoria</u> x King Island	1.45 (15, 6)	ns
	♀ <u>Victoria</u> x Flinders Island	1.62 (15,11)	ns
	♀ King Island x Flinders Island	1.12 ( 6,11)	ns
	♀ <u>Victoria</u> x <u>Tasmania</u>	4.05 (15,14)	**
	♀ King Island x <u>Tasmania</u>	2.79 ( 6,14)	ns
	♀ Flinders Island x <u>Tasmania</u>	2.50 (11,14)	ns
<u>Acanthiza ewingi</u> and <u>pusilla</u>	♂ <u>Victoria</u> x <u>ewingi</u> King Island	1.05 (29,14)	ns
	♂ <u>Victoria</u> x <u>ewingi</u> Flinders Island	2.34 ( 8,29)	*
	♂ King Island x <u>ewingi</u> Flinders Island	2.46 ( 8,14)	ns
	♂ <u>Victoria</u> x <u>ewingi</u> <u>Tasmania</u>	1.22 (35,29)	ns
	♂ <u>Victoria</u> x <u>pusilla</u> <u>Tasmania</u>	2.80 (27,29)	**
	♂ <u>ewingi</u> King Island x <u>ewingi</u> <u>Tasmania</u>	1.29 (35,14)	ns
	♂ <u>ewingi</u> Flinders I. x <u>ewingi</u> <u>Tasmania</u>	1.91 ( 8,35)	ns
	♀ <u>Victoria</u> x <u>ewingi</u> King Island	1.37 ( 6, 6)	ns
	♀ <u>Victoria</u> x <u>ewingi</u> Flinders Island	1.54 ( 6, 5)	ns
	♀ <u>ewingi</u> King I. x <u>ewingi</u> Flinders I.	1.13 ( 6, 5)	ns
	♀ <u>Victoria</u> x <u>ewingi</u> <u>Tasmania</u>	1.02 (11, 6)	ns
	♀ <u>Victoria</u> x <u>pusilla</u> <u>Tasmania</u>	1.49 (17, 6)	ns
	♀ <u>ewingi</u> King Island x <u>ewingi</u> <u>Tasmania</u>	1.39 (11, 6)	ns
	♀ <u>ewingi</u> Flinders I. x <u>ewingi</u> <u>Tasmania</u>	1.57 (11, 5)	ns
<u>Meliphaga leucotis</u> and <u>flavicollis</u>	♂ <u>Victoria</u> x King Island	1.72 ( 8,29)	ns
	♂ <u>Victoria</u> x Flinders Island	1.33 (29, 6)	ns
	♂ King Island x Flinders Island	2.29 ( 8, 6)	ns
	♂ <u>Victoria</u> x <u>Tasmania</u>	2.18 (47,29)	**
	♂ King Island x <u>Tasmania</u>	1.27 (47, 8)	ns
	♂ Flinders Island x <u>Tasmania</u>	2.90 (47, 6)	ns
	♀ <u>Victoria</u> x King Island	1.05 (16, 5)	ns
	♀ <u>Victoria</u> x <u>Tasmania</u>	1.42 (16,38)	ns
	♀ King Island x <u>Tasmania</u>	1.35 ( 5,38)	ns
<u>Melithreptus lunatus</u> and <u>affinis</u>	♂ <u>Victoria</u> x <u>Tasmania</u>	1.11 (42,23)	ns
	♀ <u>Victoria</u> x <u>Tasmania</u>	1.71 (22, 8)	ns
<u>Melithreptus gularis</u> and <u>validirostris</u>	♂ <u>Victoria</u> x King Island	2.16 ( 9, 5)	ns
	♂ <u>Victoria</u> x <u>Tasmania</u>	12.50 (21, 5)	**
	♂ King Island x <u>Tasmania</u>	5.78 (21, 9)	**

Note: ns, \*, \*\* respectively give the significance of a difference as  $P > 0.05$ ,  $0.05 > P > 0.01$ , and  $0.01 > P > 0.001$ .



APPENDIX TABLE 2B

SIGNIFICANCE OF DIFFERENCES IN VARIATION IN TARSAL LENGTH BETWEEN ISLAND AND MAINLAND POPULATIONS. CONVENTIONS AS FOR APPENDIX TABLE 2A.

Species	Localities	F (df)	P
<u>Malurus cyaneus</u>	♂ <u>Victoria x King Island</u>	1.42 (52,57)	ns
	♂ <u>Victoria x Flinders Island</u>	2.45 (52,16)	*
	♂ <u>King Island x Flinders Island</u>	1.72 (27,16)	ns
	♂ <u>Victoria x Tasmania</u>	1.27 (52,71)	ns
	♂ <u>King Island x Tasmania</u>	1.12 (71,27)	ns
	♂ <u>Flinders Island x Tasmania</u>	1.93 (71,16)	ns
<u>Sericornis frontalis</u> / <u>S. humilis</u>	♂ <u>Victoria x King Island</u>	3.17 (30,19)	**
	♂ <u>Victoria x Flinders Island</u>	1.50 (30,17)	ns
	♂ <u>King Island x Flinders Island</u>	2.11 (17,19)	ns
	♂ <u>Victoria x Tasmania</u>	1.18 (42,30)	ns
	♂ <u>King Island x Tasmania</u>	3.74 (42,19)	**
	♂ <u>Flinders Island x Tasmania</u>	1.77 (42,17)	ns
	♀ <u>Victoria x King Island</u>	2.86 (18, 6)	ns
	♀ <u>Victoria x Flinders Island</u>	1.59 (18,11)	ns
	♀ <u>King Island x Flinders Island</u>	1.79 (11, 6)	ns
	♀ <u>Victoria x Tasmania</u>	4.53 (18,15)	**
	♀ <u>King Island x Tasmania</u>	1.59 ( 6,15)	ns
	♀ <u>Flinders Island x Tasmania</u>	2.85 (11,15)	*
<u>Acanthiza ewingi</u> and <u>pusilla</u>	♂ <u>Victoria x ewingi King Island</u>	3.08 (29,14)	*
	♂ <u>Victoria x ewingi Flinders Island</u>	6.02 (29, 8)	**
	♂ <u>ewingi King I. x ewingi Flinders I.</u>	1.96 (14, 8)	ns
	♂ <u>Victoria x ewingi Tasmania</u>	5.90 (29,35)	**
	♂ <u>Victoria x pusilla Tasmania</u>	3.34 (29,28)	**
	♂ <u>ewingi King Island x ewingi Tasmania</u>	1.92 (14,35)	ns
	♂ <u>ewingi Flinders I. x ewingi Tasmania</u>	1.02 (35, 8)	ns
	♀ <u>Victoria x ewingi King Island</u>	5.93 ( 5, 6)	*
	♀ <u>Victoria x ewingi Flinders Island</u>	5.49 ( 5, 5)	*
	♀ <u>ewingi King I. x ewingi Flinders I.</u>	1.08 ( 5, 6)	ns
	♀ <u>Victoria x ewingi Tasmania</u>	3.77 ( 5,11)	*
	♀ <u>Victoria x pusilla Tasmania</u>	1.07 ( 5,16)	ns
	♀ <u>ewingi King Island x ewingi Tasmania</u>	1.57 (11, 6)	ns
	♀ <u>ewingi Flinders I. x ewingi Tasmania</u>	1.46 (11, 5)	ns
<u>Meliphaga leucotis</u> and <u>flavicollis</u>	♂ <u>Victoria x King Island</u>	1.25 ( 8,30)	ns
	♂ <u>Victoria x Flinders Island</u>	1.74 ( 7,30)	ns
	♂ <u>King Island x Flinders Island</u>	1.40 ( 7, 8)	ns
	♂ <u>Victoria x Tasmania</u>	2.04 (49,30)	**
	♂ <u>King Island x Tasmania</u>	1.63 (49, 8)	ns
	♂ <u>Flinders Island x Tasmania</u>	1.17 (49, 7)	ns
	♀ <u>Victoria x King Island</u>	1.11 ( 8,15)	ns
	♀ <u>Victoria x Tasmania</u>	1.83 (39,15)	ns
	♀ <u>King Island x Tasmania</u>	9.03 (39, 5)	*
<u>Melithreptus lunatus</u> and <u>affinis</u>	♂ <u>Victoria x Tasmania</u>	1.50 (23,43)	ns
	♀ <u>Victoria x Tasmania</u>	1.38 (23, 9)	ns
<u>Melithreptus gularis</u> and <u>validirostris</u>	♂ <u>Victoria x King Island</u>	1.11 ( 5,10)	ns
	♂ <u>Victoria x Tasmania</u>	2.47 (21, 5)	ns
	♂ <u>King Island x Tasmania</u>	2.74 (21,10)	ns

Note: ns, \*, \*\* respectively give the significance of a difference as  $P > 0.05$ ,  $0.05 > P > 0.01$ , and  $0.01 > P > 0.001$ .